

WEB BUILDING BEHAVIOR AND THE PHYLOGENY OF AUSTROCHILINE SPIDERS

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ABSTRACT. We report on the natural history and web building behavior of the South American austrochilids *Thaida peculiaris* and *Austrochilus forsteri*, relatively basal lineages within Araneomorphae. Species of these two cribellate genera construct large, two-dimensional sheet webs with a funnel retreat. When combing cribellate silk, austrochilids use both fourth legs, like entelegyne spiders, and unlike Hypochilidae and Filistatidae. Furthermore, the alternancy of combing legs IV is determined by the leg III involved in the attachment of a cribellate segment; the leg IV ipsilateral to the leg III that made the attachment will comb the next segment, except for the first segment. This similarity to Entelegynae in combing with both fourth legs contradicts current hypotheses of basal araneomorph relationships and suggests that the Austrochilidae may be the sister group of entelegyne spiders.

Keywords: Austrochilinae, combing behavior, systematics, phylogeny

Behaviors associated with web building and web architecture itself are increasingly used as indicators of relationships among higher groups of spiders (e.g., Eberhard 1982, 1988, 1990; Coddington 1986a, 1990; Hormiga et al. 1995; Griswold et al. 1998, 1999; Scharff & Coddington 1997). The nature and disposition of sticky threads seems to be especially informative (Eberhard 1988; Eberhard & Pereira 1993). Most spiders that rely on a web for prey capture have special, adhesive threads to help retain prey until they are subdued. These sticky threads are consistently laid on a non-sticky structural scaffolding (Eberhard 1992). Two basic types of sticky threads exist, each used by different groups of spiders (e.g., Opell 1997). Dry, cribellar capture threads (Fig. 7) have fibrils produced by hundreds of minute cribellar spigots, while araneoid viscid capture threads have droplets of sticky glue produced by two pairs of aggregate gland spigots. Pholcid spiders also produce viscid silk like that of araneoids (Briceño 1985), but both anatomy and phylogeny (Platnick et al. 1991) suggest independent origins of sticky silk in pholcids and araneoids. It is well established that primitive araneomorph spiders

were cribellate (Forster et al. 1987; Platnick et al. 1991).

Eberhard (1988) observed and compiled information on combing behavior for many cribellate families. He described two basic patterns of combing behavior. In type I, observed in *Hypochilus* and Filistatidae, the combing leg IV rests on the contralateral leg III, but only leg IV moves. In type II, observed in cribellate entelegynes, the combing leg IV holds on the contralateral leg IV, and both legs move together as an almost rigid unit. Eberhard logically concluded that type II combing behavior is a synapomorphy of Entelegynae (see Fig. 18).

The subfamily Austrochilinae includes two genera endemic to temperate forests in Southern Chile and Argentina (Forster et al. 1987). They comprise, along with the austrochilid Hickmaniinae and Gradungulidae, the superfamily Austrochiloidea, the sister group of Araneoclada (all araneomorph spiders except Hypochilidae, Platnick et al. 1991). Little is known of austrochiline behavior (as is the case in most other Austrochiloidea), other than the general appearance of their webs and their nocturnal habits (Forster et al. 1987 and references therein; Ramírez & Platnick 1999). Because of their basal position, austrochiloids are especially interesting for testing the evo-

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lution of combing behavior, and may provide an insight into the origin of the sheet webs of araneomorph spiders. We present here the first data on combing behavior in Austrochilinae, and some observations on the web architecture and sequence of construction.

METHODS

Observations were made in three localities in southern Chile and Argentina, in December and January. 1) Aguas Calientes, Parque Nacional Puyehue, elev. 400–500 m, 40°44'S, 72°18'W, Osorno Province, Región X, Chile (13–17 December 1998, M. Ramírez, L. Compagnucci, C. Grismado and L. Lopardo collectors). 2) Monumento Natural Contulmo, elev. 340m, 38°01'S, 73°11'W, Malleco Province, Región IX, Chile (19–21 December 1998, same collectors as above). 3) Puerto Blest, elev. 800m, 41°02'S, 71°49'W, Parque Nacional Nahuel Huapi, Neuquén Province, Argentina (7–19 January 2000, L. Lopardo and A. Quaglini collectors). These are intensively collected localities of Valdivian temperate forest.

The spiders were observed in the field, mostly using the methods described by Eberhard (1992). We selected several large and easily accessible webs, and marked their location with brightly colored ribbons to locate them at night. During the day, we made a large hole in the central part of the sheet, leaving only the retreat and sometimes also the main lateral lines, and returned at dusk to observe repair or reconstruction. Prey capture behavior was observed on insects that came naturally to the webs, as well as others that we tossed onto intact webs when the spider was active. For photography and to facilitate detailed observations we increased contrast by dusting the webs with cornstarch (Carico 1977). Dusting also allowed observation of progress in web building by distinguishing the recent, unpowdered threads from the older ones. Observations of active spiders were made at night with a two D cell flashlight covered with two layers of red cellophane. Even with this red light, the spiders were sensitive to direct illumination. For prolonged observations we illuminated the background just enough to see the spider's outline. Although we tried to minimize disturbances, these spiders were very sensitive and timid and often fled to the retreat after 1–5 minutes of contin-

uous observation. We therefore observed either several individuals for repeated short periods within the same night, or one spider all night long, so it accommodated to the observer from the beginning of its activity period. After observations were complete, we collected the spiders for identification, although some escaped. All adult specimens from Puyehue and Puerto Blest are *Thaïda peculiaris* Karsch 1880, and those from Contulmo are *Austrochilus forsteri* Grismado, Lopardo & Platnick in press). We also collected the minute kleptoparasite spiders *Sofanapis antillanca* Platnick & Forster 1989 (Anapidae) from austrochilid webs. The webs and behavior of *Thaïda* and *Austrochilus* species appeared indistinguishable. Therefore, we present a general account that applies equally to both genera and, where possible, we identify the specimens from which observations were made. We observed more than 60 spiders in all.

Vouchers of all observations, photographic slides and web samples are labelled with acronyms of collector, date and a sequential number or code, followed by film frame number (e.g., MJR 15.XII.98/Au4, frame 9). Specimens with these labels are deposited in Museo Argentino de Ciencias Naturales (MACN-Ar, Cristina Scioscia, Buenos Aires) and Museo Nacional de Historia Natural de Chile (MHNS, Ariel Camousseight, Santiago de Chile). Web samples and photographs are deposited in MACN-Ar.

Specimens.—*Thaïda peculiaris*: Aguas Calientes, Puyehue: 1 ♂, 1 ♀ penultimate, 2 immatures (MACN-Ar 9989); 1 ♀ penultimate (no web, just the retreat) (MACN-Ar 10002); 1 ♀ (MJR 13.XII.98–1, with eggsac) (MACN-Ar 9991); 1 ♂ (CG 15.XII.98–10) (MACN-Ar 10000); 1 ♀ penultimate (Au4) (MHNS); 1 immature (Au6) (MACN-Ar 9992); 4 immatures (AuX6) (MACN-Ar 10003); 1 indefinite specimen (Au10) (MACN-Ar 9986); 1 ♂ penultimate (Au11) (MHNS); 1 immature (Au12) (MACN-Ar 9999); 1 ♀ (MJR 15.XII.98/Au13, frame C1) (MACN-Ar 9993); 1 indefinite specimen (Au17) (MACN-Ar 9997); 1 immature (MJR 14.XII.98/Au21, frame A7) (MACN-Ar 9994); 1 ♀ penultimate (Au24) (MHNS); 1 indefinite specimen (Au27) (MACN-Ar 10005); 1 ♀ (MJR 16–17.XII.98/Au28A, frames C5, D20) (MACN-Ar 9990); 1 ♀

(Au28B) (MACN-Ar 9998); 1 immature (Au29) (MACN-Ar 10004); 1 ♂ penultimate (Au30) (MHNS); 1 ♀ penultimate (Au31) (MACN-Ar 9985); 1 immature (Au32) (MHNS); 2 indefinite specimens (Au33) (MACN-Ar 9995); 1 indefinite specimen (Au38) (MACN-Ar 9988); 1 immature (Au40) (MACN-Ar 9996); 1 indefinite specimen (Au41) (MACN-Ar 10006); 1 ♀ (Au42B) (MACN-Ar 9987). Puerto Blest: 4 ♀: Au1 (MACN-Ar 9976), Au6 (MACN-Ar 9979), Au9 (MACN-Ar 9977), Au10 (MACN-Ar 9978); 1 ♀ penultimate: Au3 (MACN-Ar 9984); 1 immature: Au7 (MACN-Ar 9980); 3 ♂ penultimate: Au4 (MACN-Ar 9983), Au8 (MACN-Ar 9981), Au11 (MACN-Ar 9982).

Austrochilus forsteri: Monumento Natural Contulmo: 1 male holotype (MHNS); 1 female paratype (MJR 19.XII.98/10; MHNS); 1 ♀, 2 immatures (MHNS); 1 ♀ 4 immatures (MACN-Ar 9845); 1 immature (MACN-Ar 9846); 2 immatures (MHNS); 1 immature (MJR 19.XII.98-7; MACN-Ar 9844); 1 immature (MJR 19.XII.98-9; MACN-Ar 9847); 1 ♀ (MJR 19.XII.98-11, frame E30; MACN-Ar 9839); 1 ♀ (AuX1; MACN-Ar 9838); 1 ♂ (AuX2; MACN-Ar 9837); 1 immature (AuX3; MACN-Ar 9841); 1 immature (AuX4; MACN-Ar 9842); 1 ♂ penultimate (AuX5; MACN-Ar 9840); 1 immature (AuX7; MACN-Ar 9843); 1 ♀ penultimate (AuX8; MHNS).

Sofanapis antillanca Platnick and Forster: Aguas Calientes, Puyehue: On web of *Austrochilinae*: 2 ♂, 3 ♀, 3 immatures (MHNS), 2 ♂, 3 ♀, 3 immatures (MHNS), 2 ♂, 2 immatures (MJR 15.XII.98/2; MACN-Ar), 1 immature (MACN-Ar); 1 ♀ (LL&MJR 15.XII.98/1 on web of *Austrochilinae* Au4, web sampled; MACN-Ar); 1 immature (on web of *Austrochilinae* Au11; MACN-Ar); 1 ♂, 1 ♀, 4 immatures (on web of *Austrochilinae* Au12; MHNS); 3 ♀, 2 immatures (on web of *Austrochilinae* Au13, two *Sofanapis* escaped; MHNS); 2 immatures (on web of *Austrochilinae* Au17; MACN-Ar); 3 ♀, 2 immatures (on web of *Austrochilinae* Au27; MHNS); 1 ♂, 4 ♀, 2 immatures (on web of *Austrochilinae* Au31; MACN-Ar); 4 immatures (on web of *Austrochilinae* Au40; MACN-Ar). Monumento Natural Contulmo: 1 ♀ (MHNS); 1 ♀ (MACN-Ar). On web of *Austrochilinae*: 27 ♀, 6 ♂ (MACN-Ar); 5 ♂, 2 ♀, 2 immatures (MHNS); 1 ♂, 6 ♀, 2 im-

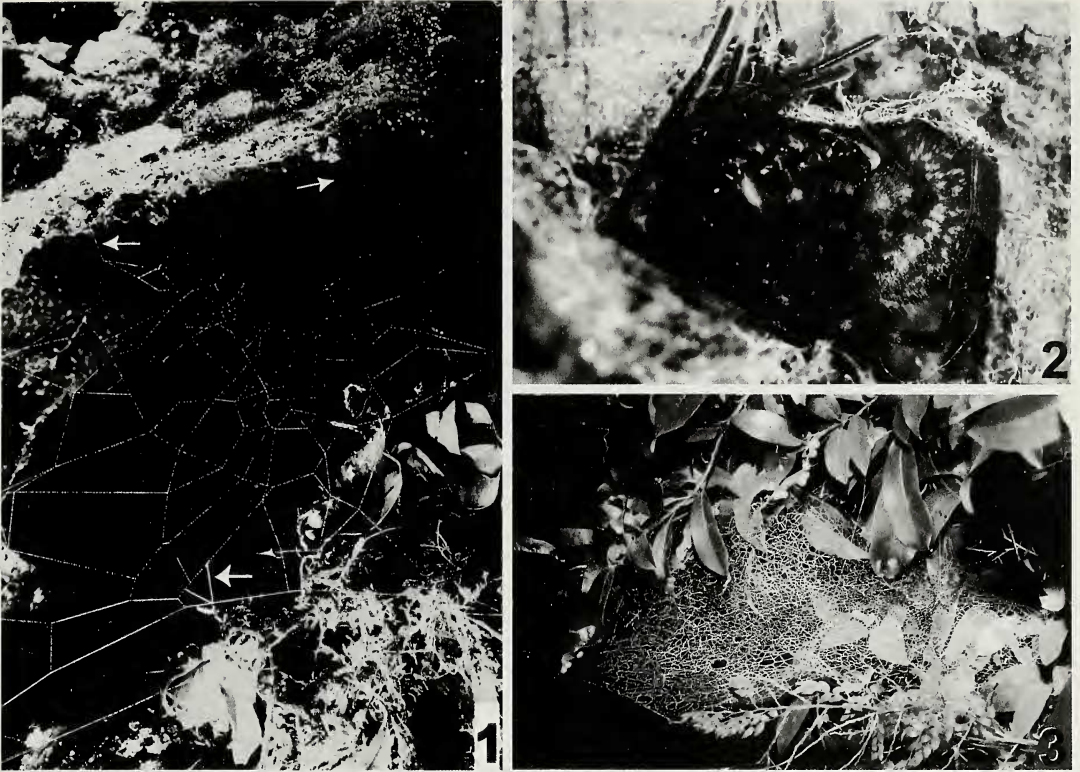
matures (MHNS); 2 ♀ (MJR 19.XII.98/7, on web of *Austrochilinae* same reference; MACN-Ar); 2 ♂, 6 ♀, 1 immature (on web of *Austrochilinae* MJR 19.XII.98/10; MACN-Ar); 2, 7 ♀ (web sampled, on web of *Austrochilinae* Au100; MACN-Ar). 1 ♂, 2 ♀ (MJR 21.XII.98/9 on *Porteria* sp. web, same reference; MACN-Ar); 1 ♀ (MJR 21.XII.98/10 on *Porteria* sp. web, same reference; MACN-Ar).

RESULTS

Thaïda and *Austrochilus* species build large, horizontal or slightly sloping, permanent sheet webs with retreats (Figs. 1, 3, 4). Web size varies greatly (about 50–120 cm), but seems to correlate with specimen size. *Austrochilines* enlarge the web by adding to its edge on successive nights, at least during the first days of construction. Web shape varies according to available space and attachment points. The distance from the ground to the sheet and refuge ranges from very short (when the external border of the web is attached to the soil) to more than two meters high. A normal web consists of three components: an exposed horizontal sheet, several vertical supporting lines near the retreat (Figs. 1 & 13; thin and thick arrows respectively), and a hidden tube-like retreat (Fig. 4) connected to the sheet by a funnel. Two kinds of thread comprise the sheet: non-sticky supporting lines, and sticky cribellate lines. The mesh cells of the sheet are rather uniform, but the sticky and non-sticky lines do not form any obvious regular pattern or orientation.

The spiders spend the day inside their retreats, which are often inaccessible, deep within tree trunks or rock crevices. If the retreat is opened, or after serious disturbance, they assume a cryptic posture with all legs tightly flexed (Fig. 2), as is typical of most web building araneomorphs, including *Hypochilus* and gradungulids (Shear 1969; Forster et al. 1987). Near sunset, they move to the opening of the retreat, with the abdomen facing outward (Fig. 4). Activity begins right after sunset (about 21:00, summer), when the spiders turn facing outwards. At about 22:00 they gradually emerge onto the sheet and begin activities such as cleaning the web, rebuilding damaged areas, catching prey and feeding, expanding the sheet, or adding sticky silk.

Non-sticky scaffolding.—To elicit web-building behavior, we destroyed the entire



Figures 1–3.—*Austrochilus forsteri* and web of *Thaidia peculiaris*. 1. *Thaidia peculiaris*, non-sticky scaffolding dusted with cornstarch, upper view. Thin arrows to the vertical supporting lines, thick arrow to first cribellate thread (MJR 14.XII.98/Au21 frame A7, Puyehue). 2. *Austrochilus forsteri*, cryptic posture after disturbance (MJR II.92 frame 807, Contulmo). 3. *Thaidia peculiaris*. Webs general appearance (GH 31.XII.2000/ frame Ph9/R5, dusted, Puyehue). Photo by Gustavo Hormiga.

sheet of several *T. peculiaris* from Puyehue, leaving only a few marginal lines attached to the retreat (in one penultimate female (Au31), two penultimate males (Au30, Au39), two immatures (Au40, Au29), and two indeterminate specimens (Au32, Au38). We observed only two individuals (Au31 and Au38) making the first lines of the non-sticky scaffolding, thus these data are preliminary. In general, the pattern observed seems to be similar to the horizontal “extension of the skeleton web” as described by Eberhard for the pholcid *Modisimus guatuso* Huber (Eberhard 1992; Huber 1998). The spiders began by laying two horizontal lines, one on each side from the retreat, thus forming an open “V”. Then they attached a new non-sticky line distally to the right line, walked along this line, passed in front of the retreat, and walked a short distance along the left line before attaching the new thread (e.g. L1), thus delimiting an irregular triangle. They then walked further out on

the same line, made another attachment, and returned to L1 and attached the thread to it, thus making another triangle. As the spiders repeated this process, the non-sticky scaffolding gradually expanded outward from the retreat. At this point, both spiders detected our presence and stopped building or returned to the retreat, so that subsequent observations are fragmentary. At some point after the initial extension of the sheet the spiders must begin to subdivide the original triangles with non-sticky threads, gradually making a homogeneous, uniform, open scaffolding. Building behavior frequently alternated with pauses or slow movements without attachment. The spiders built most of the non-sticky scaffolding on the first night and adding cribellate sticky threads on following nights. Other undisturbed specimens laid both the support and some cribellate lines in the first night. We do not know how the vertical supporting lines near the retreat are laid.



Figures 4–5.—*Thaida peculiaris* from Puyehue, feeding on a wrapped prey. Many *Sofanapis antillanca* are around the prey (MJR 16.XII.98/Au37). 4. Holding prey in the retreat opening. The abdomen is orientated outward (frame C26). 5. Same. Many *Sofanapis antillanca* are descending from the sheet to land on the prey (frame C18).

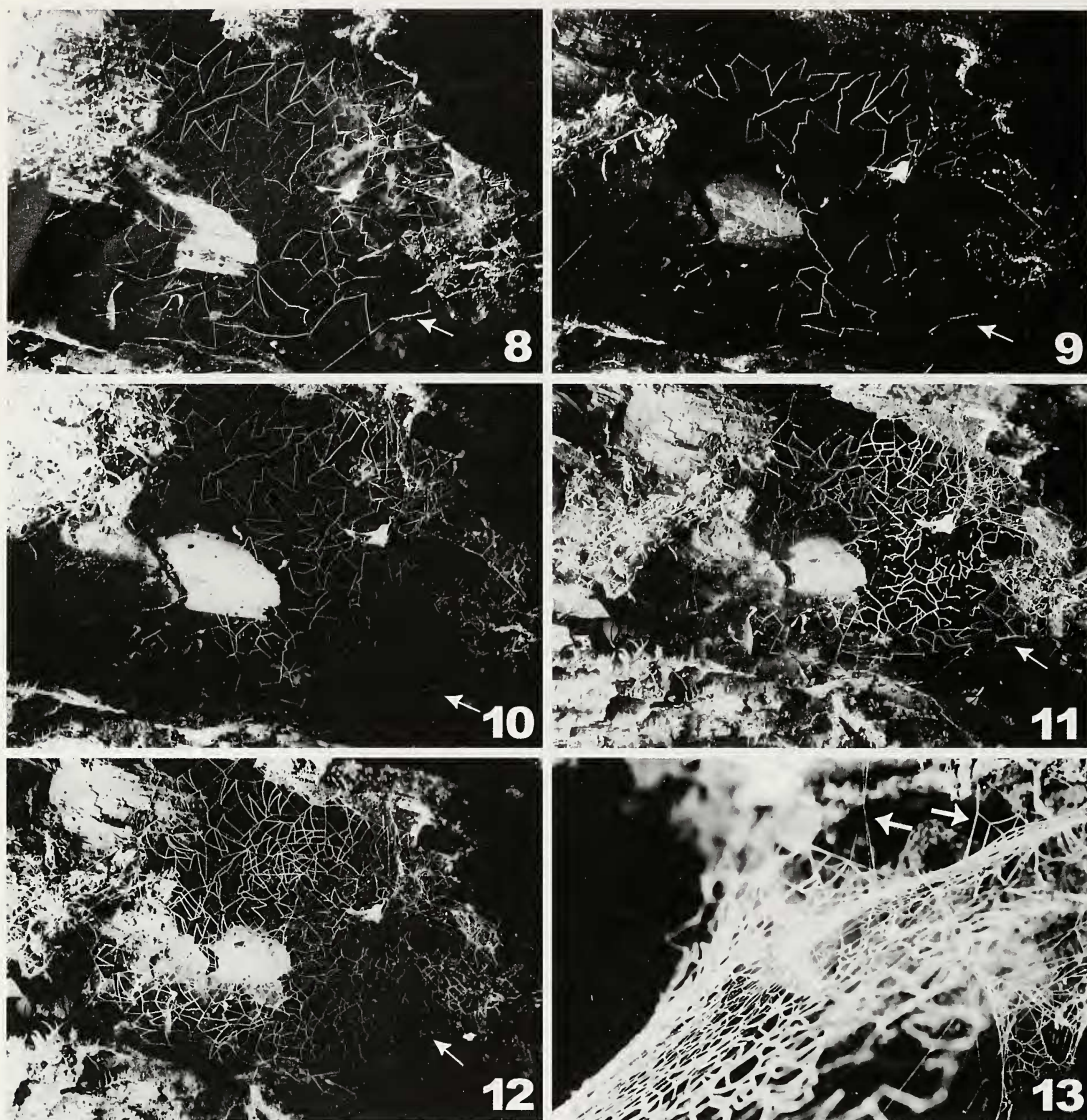


Figures 6–7.—*Austrochilus forsteri* female combing a cribellate thread (MJR 19.XII.98/11 frame E30, Contulmo). 6. The right leg III is holding the last attachment position, the left leg III is testing threads where the next attachment will be made. 7. Same, detail of the cribellate thread.

Sticky lines and combing.—Combing behavior is performed at intervals, usually starting at 22:30, and continuing to at least 05:00. The spider combs with one leg IV and attaches the sticky thread to a non-sticky line held with either leg III. The tarsus-metatarsus joint of the contralateral leg IV supports the combing leg IV, and they move simultaneously as an almost rigid unit (Fig. 6, type II combing of Eberhard 1988). As the spider combs, it moves slowly forward, gently exploring with legs III, apparently probing for a non-sticky line to which the cribellate thread will be attached. Once the sticky segment is spun, the spider stops, one leg III grasps the non-sticky line near the future point of attachment, the abdomen rises towards that point, and the cribellate thread is attached with the spinnerets. Legs IV do not touch the web at that moment and are not involved in attachment. The first attachment before combing begins is made on the line held by either leg III, and then the spider starts to comb the cribellate silk with one leg IV (usually ipsilateral to the leg III that guided the attachment), then attaches the sticky segment adjacent to either leg III, and then always combs the next segment with the ipsilateral leg IV. Completed sticky lines are

always attached to a line held by a leg III, and so on. Commonly, left and right legs III alternate consecutive attachments, forming a zig-zag pattern, but this often varies (Figs. 9, 14). However, the leg III involved in attachment consistently determines that the ipsilateral leg IV will comb the next segment (except for the first segment in a bout of sticky silk construction). Thus, if two consecutive segments are attached using the same leg III, they are combed with the same ipsilateral leg IV.

Occasionally the spider switches the combing leg IV during the spinning of one segment, suggesting a preference to comb with a particular leg. One *T. peculiaris* female (Puerto Blest, Au9) clearly tended to comb with the left leg IV. Once it started to comb with the disfavored (i.e. right) leg (as implied by the prior attachment with right leg III), the spider soon switched to the “preferred” left combing leg and continued combing the same segment. In 34 observed sticky silk segments, 17 segments were made with left legs III and IV, five with right legs III and IV, 11 segments were begun with the right leg IV but soon switched to left leg IV, and just one segment started



Figures 8–13.—*Thaida peculiaris* from Puyehue, successive stages of the same web; arrows of the same type indicate same threads (MJR 15–17.XII.98/Au20). 8. Non-sticky scaffolding and first cribellate threads, with cornstarch, first night. (frame B16). 9. Second night, without further cornstarch (new cribellate threads are not visible). Note the alterations on previous cribellate threads (frame C14). 10. Same as 9, with cornstarch making visible the cribellate threads of first and second night (frame C15). 11. Third night, without further cornstarch (frame D13). 12. Same as 11, with cornstarch. Note the extension of the left and the bottom-right edges (frame D14). 13. Third night, lateral view near the retreat's mouth roof, showing slope and vertical supporting lines (thick arrows) (frame D16).

with left leg IV and near the end switched to right leg IV.

Cribellate lines in webs usually zigzag (Figs. 8–12, 14), angling sharply at the attachment points. This pattern probably occurs because the animals tend to alternate left and right third legs when attaching. Occasionally,

two consecutive sticky silk attachments are made on the same non-sticky line, so that sticky and non-sticky lines run as one (Fig. 14, arrow). This behavior is similar to that described by Eberhard (1988) for *Psechrus* (Psechridae). We perceived no definite overall trajectory during cribellate silk-spinning bouts;

the zigzags may rotate or be interrupted without any apparent regularity (Figs. 8, 14). However, the spiders commonly place the first cribellate lines near the outer edge (e.g., thick arrow in Fig. 1). The mesh of the sheet becomes denser from night to night, as more cribellate threads are laid.

Adding new lines at the edges of the web.—One or two-night old sheets are typically smaller than older webs. We marked the edges of several recently made sheets with cornstarch, and returned the following day (or night) to see the new lines. The spider extended the sheet from the borders (compare Figs. 8–12, arrows). The spider continues to expand the sheet in subsequent nights, first adding new non-sticky supporting structure to the outer edge, and afterwards the cribellate silk.

Cleaning the sheet.—Webs are usually quite clean, in spite of considerable accumulation of detritus during the day. We observed cleaning behavior in many individuals. Having touched an entangled object, the spider pulls it down with the palps and legs I and II, and cuts entangling threads one by one, apparently with the chelicerae. The object is drawn through the resulting hole in the sheet, handled with palps and forelegs, and dropped. The spider then repairs the hole.

Rebuilding the damaged patches of the web.—As has been observed in other cribellate spiders (due to “fabricational (constructional) constraints”, Seilacher 1973; Coddington 1986b), austrochilines first build the non-sticky scaffolding, and then the cribellate threads, both during web construction and during web repair. Holes in the sheet due to cleaning, prey, or made artificially by us, were all repaired the same way. The spider spins a non-sticky supporting mesh similar to the normal one, and then adds cribellate silk.

Territoriality and aggression.—Webs are individual, occur quite close to each other, but do not share threads. On three occasions, we observed two *T. peculiaris* (in Puyehue, Au41) on the same web. In each case, the larger owners were near their retreats, and the smaller visitor walked slowly at the periphery of the sheet. The owner made no response, and the foreign spider shortly went away. We saw several males (Fig. 15) walking near the retreats of females. In one case a male approached a female guarding an eggsac (in

Puyehue, Au42B), and they started touching each other with legs I and II, the male vibrated his body at intervals. The male went away and soon returned near to the female. The female seemed neither receptive nor aggressive. Many individuals were collected by hand and never tried to bite. It seems that austrochilids are neither very territorial nor aggressive.

Attack and feeding.—Several individuals fed on beetles, flies and moths subequal to the spider's body size or smaller. Much smaller insects, such as mosquitoes, were ignored. The spider usually runs towards an entangled prey and bites it repeatedly, then leaves it for a while. After a delay, the spider approaches the immobile prey and transfers it to the lower web surface in order to handle and carry it to the retreat for feeding (Fig. 4). Sometimes animals remain on the sheet for feeding. Prey may or may not be wrapped before eating (the prey in Fig. 5 was wrapped). An immature *T. peculiaris* (Puerto Blest, Au7) bit a moth, passed it through the sheet, and then wrapped it with alternating legs IV. The moth (still partially entangled) was held with legs III, palps, and sometimes with a leg II, thus the spider hung from the web only by legs I. After that, the spider held the moth with legs I and II while feeding on it, hanging from the sheet only by legs IV and sometimes III. It alternated wrapping and feeding for six consecutive hours; and then, near sunrise, dropped the prey and went to the retreat.

Eggsacs.—Oviposition seems fairly synchronous because all eggs collected from the same locality were at a similar developmental stage (observed as in Holm 1940) (in another field trip in Argentina, Neuquén Province, Quetrihué, 24 February 1996, MJR found all eggsacs of *T. peculiaris* empty). Eggsacs are laid in protected places not associated with webs, or near the retreat, but never inside it. They are ovoid (ca. 4 cm long and 2.5 cm wide) and hang from a pedicel (Fig. 17). They have an internal lining of white, finely meshed silk, and are externally covered by cribellate silk, non-sticky silk, and detritus. We saw one female *T. peculiaris* (in Puyehue, Au28B) combing and attaching cribellate silk to the eggsac, as has been seen in many other entelegyne spiders (e.g., Peters & Kooor 1989; Kraus 1988). Females remain near their own eggsacs and may or may not maintain a sheet web while guarding eggs. The guarding fe-



Figures 14–17.—*Thaida peculiaris* from Puyehue. 14. Detail of sticky thread. Note the sticky thread laid along a non-sticky line (arrow) (MJR 15.XII.98/Au14 frame B9). 15. Male on web of female Au13 (MJR 15.XII.98/Au13 frame C1). 16. Closed retreat of female guarding an eggsac, without sheet web (arrow to retreat; an orb-web of the tetragnathid *Metabus* sp. covers the entire area) (MJR 16.XII.98/Au28A frame C5). 17. Eggsac, same as before, after removing the protection web (MJR 17.XII.98/Au28A frame D20).

males of *T. peculiaris* in Puerto Blest maintain normal sheets, but those in Puyehue, and the guarding females of *A. forsteri* in Contulmo, lacked sheets. Those lacking a sheet had a vertical barrier covering the entrance of the retreat (Fig. 16). Some females may have moved from their original retreats to lay the eggsac, because some *T. peculiaris* (in Puyehue) were found in atypical, more exposed places, such as isolated trees without any nearby point to which to attach a sheet. It is not clear how the spiderlings manage to leave the eggsac.

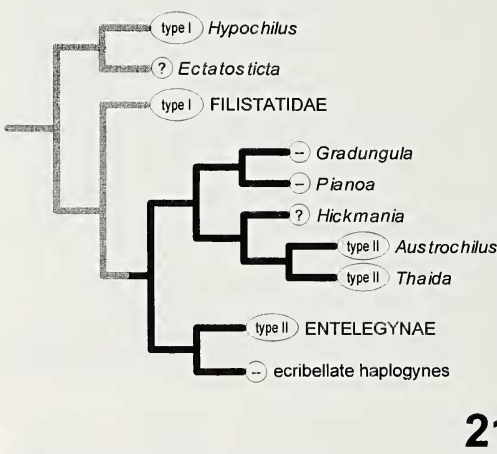
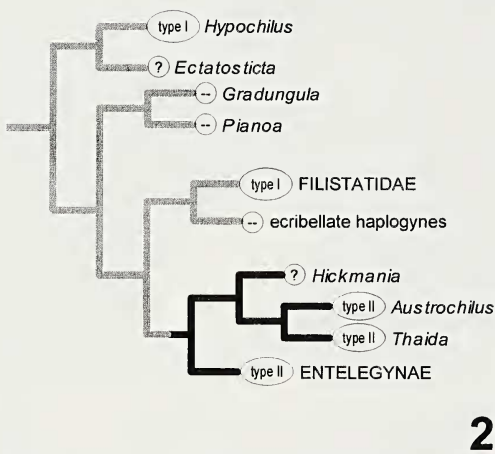
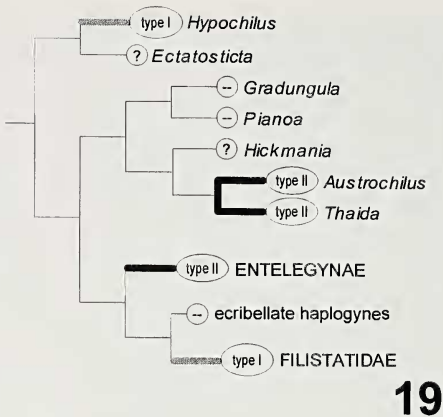
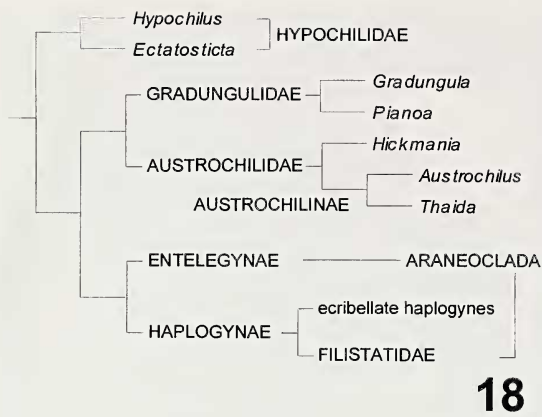
Kleptoparasites.—The anapid kleptoparasitic spider *Sofanapis antillanca*, infested all but one of the observed Chilean *T. peculiaris* and *A. forsteri* webs, with a number of individuals that varied from 1–33 individuals per host web. *Sofanapis antillanca* is known from very humid localities in Chile, but it was never found on any *T. peculiaris* web in Puerto Blest, the most humid forest locality in Argentina (Ramírez & Platnick 1999). They usually occur near the mouth of the retreat, but were seen feeding on the host's prey only at night (Figs. 4, 5). Once we saw a female *T. peculiaris* (Puyehue, Au37) trying to remove the anapids from the prey with its legs. A few *S. antillanca* were collected on the sheet webs of a *Porteria* species (Desidae) in Contulmo, but never in high densities.

Cladistic analysis.—We scored the data matrix of haplogyne spiders by Platnick et al. (1991) as modified by Ramírez (2000) for a binary character expressing the two types of combing behavior (0: type I; 1: type II). *Hypochilus* and the filistatid genera *Kukulcania* and *Filistata* (MJR, pers. obs.) have state 0; the state for *Progradungula* and *Macrogradungula* (Gradungulidae), and *Pikelinia* (Filistatidae), *Ectatosticta*, *Hickmania*, ecribellates and the root vector is unknown or inapplicable (missing entries); all other cribellates (entelegynes) and the austrochilids *Austrochilus* and *Thaïda* have state 1. The analysis of this data matrix (using the same analytical procedures as in Ramírez 2000) yields the same cladogram unaltered (Figs. 18, 19). The Bremer support for Araneoclada, however, decreases from 4.8 to 3.3 units of fit (under constant of concavity $K = 3$; length = 245 steps; Fit = 920.4; CI = 0.51; RI = 0.79).

DISCUSSION

Our observations on Austrochilinae agree with previous knowledge about the general sequence of construction of a non-sticky scaffolding followed by the addition of sticky silk (Eberhard 1992). Austrochilinae webs resemble those of *Psecchus* (Robinson & Lubin 1979), and the basic structure resembles many cribellate entelegynes, such as amphinectids and titanocids (*Metaltella* Mello-Leitão, *Goeldia* Keyserling, MJR & LL pers. obs.). Stereotyped type II combing behavior in austrochilines is, however, quite surprising, because the phylogenetic position of austrochiloids implies that they should have type I combing behavior. Combing behavior optimizes as type II at the entelegyne node and at the ancestor of *Austrochilus* + *Thaïda* of the Platnick et al. (1991) phylogenetic tree (Fig. 19). Type I occurs in *Hypochilus* and Filistatidae, but the combing behavior is ambiguous for all other internal nodes (Fig. 19). This ambiguity has two equally parsimonious reconstructions: either type II combing behavior originated independently in Entelegynae and Austrochilinae, or type I originated independently in filistatids and *Hypochilus* (Fig. 19). However, current reexamination of some internal anatomical features (such as the presence of small posterior booklungs in early stages of the filistatid *Kukulcania hibernalis*; MJR pers. obs.), and current investigations on the outgroups of the Entelegynae (Griswold et al. in prep.) suggests two other possible hypotheses (Figs. 20, 21), each implying different predictions for the combing behaviors for cribellate gradungulids. In one resolution, Austrochilidae is closer to entelegynes than to Gradungulidae (Fig. 20), thus predicting type I combing behavior for cribellate gradungulids. In the other (Fig. 21), Filistatidae is sister to all other Araneomorphae except Hypochilidae, predicting the derived type II combing behavior in cribellate gradungulids.

Data on the combing behavior of other cribellate Austrochiloidea (*Progradungula* Forster & Gray, *Macrogradungula* Gray, and *Hickmania* Gertsch), as well as the ultrastructure of their cribellate silk (Eberhard & Pereira 1993) may help to resolve the phylogeny of basal Araneomorphae and the evolution of web architecture in spiders. Thus far reconstructing the primitive spiders webs is difficult



Figures 18–21.—Different hypotheses and predictions related to combing behavior. 18. Cladogram of major groups of Araneomorphae and basal cribellates, according to Platnick et al. (1991) and Ramírez (2000). 19. Types of combing behavior optimized on the cladogram of Fig. 18. 20. One possible resolution: Austrochilids are most closely related to entelegynes than to Gradungulids. 21. Another alternative topology: Filistatids are the sister group of all other Araneomorphae except Hypochilidae.

because most key taxa build such different webs that comparisons are not straightforward. *Hypochilus* construct “lamp-shade” webs (Shear 1969), quite different from those of any other spiders (except the obviously derived webs of some stiphidiids, Gray 1992). The other hypochiloid genus, *Ectatosticta*, builds a large two-dimensional sheet web (Peter Jäger, pers. comm.). Ecribellate gradungulids do not spin webs, but cribellate species make highly modified snares, reminiscent of the ogre-faced deinopid spiders (Coddington 1986c; Gray 1983; Forster et al. 1987). Filistatines construct funnel webs (Eberhard 1988). Fortunately enough, *Hickmania troglodytes* constructs a sheet web quite similar to

that of austrochilines (Hickman 1967; Forster et al. 1987; Doran et al. 2001).

The acquisition of ampullate gland spigots by the Araneomorphae may have played an important role in spider phylogeny. Spiders use these glands to produce thin, strong cables to support their weight, manipulate prey, and construct structures that support specialized, adhesive fibers. Aerial webs are seemingly an acquisition of araneomorph spiders (the derivative webs of some mygalomorphs excepted), but the details of their evolution remain so far elusive.

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